ON THE TAXONOMY AND ULTRASTRUCTURE OF THE FOSSIL DIATOM *GOMPHONEIS CANTALICA*

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ABSTRACT. – Previous reports on the valve structure and taxonomy of the diatom *Gomphoneis cantalica* (Brun & Hérib.) M. Schm. are compared to observations made on isotype material with light and scanning electron microscopy. In particular, the number and position of the longitudinal lines are investigated and shown to be formed by internal siliceous expansions, similar to those observed in other *Gomphoneis* species. *Gomphoneis cantalica* is shown to also possess a marginal lamina which extends internally from approximately the valve margin to the edge of the valve mantle. Chambers are formed between the outer wall and lamina. Additional valve features are illustrated with the SEM. Despite having striae composed of single rows of puncta, *G. cantalica* appears ultrastructurally most similar to typical *Gomphoneis* species, thus seems best placed in this genus.

RÉSUMÉ. – Des observations antérieures sur la structure de la valve et sur la taxonomie de la diatomée *Gomphoneis cantalica* (Brun et Hérib.) M. Schm. sont comparées avec celles faites sur des isotypes en microscopie photonique et électronique à balayage. En particulier, le nombre et la position des lignes longitudinales sont étudiées et identifiées comme étant formées par des expansions siliceuses internes, semblables à celles observées chez les autres espèces de *Gomphoneis*. Il est également montré que *Gomphoneis cantalica* possède une lamina marginale qui s'étend, sur la face interne, du bord de la valve à la marge à la courbure face valvaire-manteau. Des chambres existent entre la paroi externe et la lamina. Des caractères additionels de la valve sont illustrés à l'aide du microscope électronique à balayage. Bien qu'ayant les stries composées de rangs simples de ponctuations, *G. cantalica* apparaît, du point de vue ultrastructural, comme très semblable aux espèces typiques du genre *Gomphoneis* et doit donc être placé dans ce genre.

KEYS WORDS : *Gomphoneis cantalica*, fossil diatom, taxonomy, ultrastructure, Miocène, Cantal (France).

INTRODUCTION

Previous light microscopic observations on the diatom *Gomphoneis cantalica* (Brun & Hérib.) M. Schm. (1899) have led to differing interpretations, concerning both its valve construction and its taxonomic position. Described from

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upper Miocene deposits of Aurillac, Cantal, France, this species was originally placed in the genus *Gomphonema* C. A. Agardh (1824), and distinguished from other species on the basis of its large size, striae of single rows of puncta and shadow lines running longitudinally on either side of the axial area (BRUN & HÉRIBAUD *in* HÉRIBAUD, 1893). In the next year CLEVE (1894) erected the diatom genus *Gomphoneis*, in which he included large *Gomphonema* species that possess longitudinal lines and striae composed of double rows of puncta. At that time CLEVE (1894, p. 190) commented that *G. cantalicum* was not to be included in his new genus, «... as the striae are composed of simple rows of puncta». In his discussion of this species Cleve noted a single longitudinal line on each side of the axial area, located midway between the raphe and margin. SCHMIDT (1899) later made the new combination *Gomphoneis cantalica* (Brun & Hérib.) M. Schm., apparently being of the opinion that the feature of longitudinal lines shared between *G. cantalica* and Cleve's *Gomphoneis* species was more indicative of relationships than puncta number in the striae. Recently DAWSON (1974) and others have expressed the opposite view, that the number of puncta comprising the striae may be important in indicating relationships, by transferring doubly-punctate species of *Gomphonema* that possess no longitudinal lines to *Gomphoneis*.

The longitudinal lines of *G. cantalica*, as depicted by SCHMIDT (1899), appear to be represented by one line on either side of the axial area, found near mid-valve (as indicated by Cleve). Illustrated also is a highly thickened valve outline (SCHMIDT, 1899). SCHMIDT (1899) suggested chambers associated with the longitudinal lines appeared similar to those found in some *Pinnularia* Ehrenberg (1841) species. In his review of diatoms which possess longitudinal lines, HUSTEDT (1935) arrived at the same conclusion as Schmidt concerning the classification of *G. cantalica*. Unlike Schmidt, HUSTEDT (1935, fig. 18) noted the presence of two longitudinal lines on either side of the axial area, and depicted them closely placed to one another in the central part of the valve.

These results indicate differences in evaluation of both the number and position of the longitudinal lines, and the taxonomic status of *Gomphoneis cantalica*. The present report utilizes light microscopy (LM) and scanning electron microscopy (SEM) to reinvestigate valve features of *G. cantalica*, providing ultrastructural information to aid interpretation of light microscopic observations and help clarify the classification of this enigmatic species.

MATERIALS AND METHODS

Isotype material of *Gomphoneis cantalica* (Brun & Hérib.) M. Schm. was provided by Dr. Charles W. Reimer, from the Boyer Collection of the Academy of Natural Sciences of Philadelphia (Boyer Misc. Mat. Box 4, 161, «France Diatomées fossiles d'Auvergne Dépot d'Aurillac Murat (Cantal) Miocene Supérieur from Héribaud coll. leg. Fr. Arsène. Cleaned 11 July 1920, H.C. Wheeler, Montreal»). Dried material was suspended in distilled water and air-dried onto

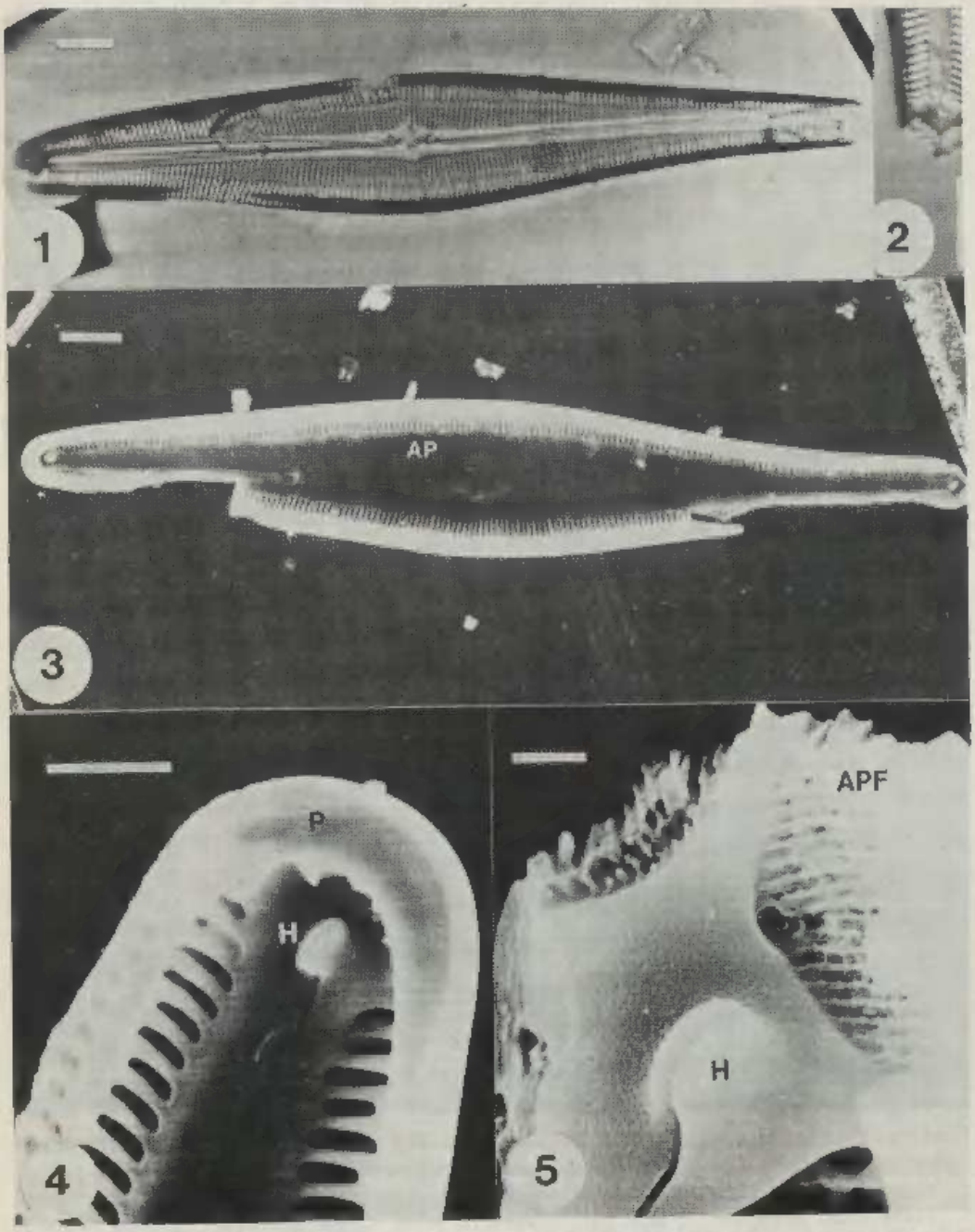

Plate I : *Gomphoneis cantalica*. — Fig. 1, 2. Light Microscopy. Fig. 1. Valve view, illustrating valve outline, filamentous raphe and position of longitudinal lines (arrows). Scale bar : 10 µm. Fig. 2. Bilobed APF with distal raphe end curving between lobes. Scale bar : 10 µm. Fig. 3-5. SEM, Internal views. Fig. 3. Valve showing structure dominated by expanded axial plate (AP). Also evident are numerous interstriae and helictoglossae at the poles. Scale bar : 10 µm. Fig. 4. Headpole, with lip-like helictoglossa (H) and pseudoseptum (P). Scale bar : 5 µm. Fig. 5. Footpole, with helictoglossa (H) and cross-shaped axial area delimiting bilobed apical pore field (APF). Scale bar : 1 µm.

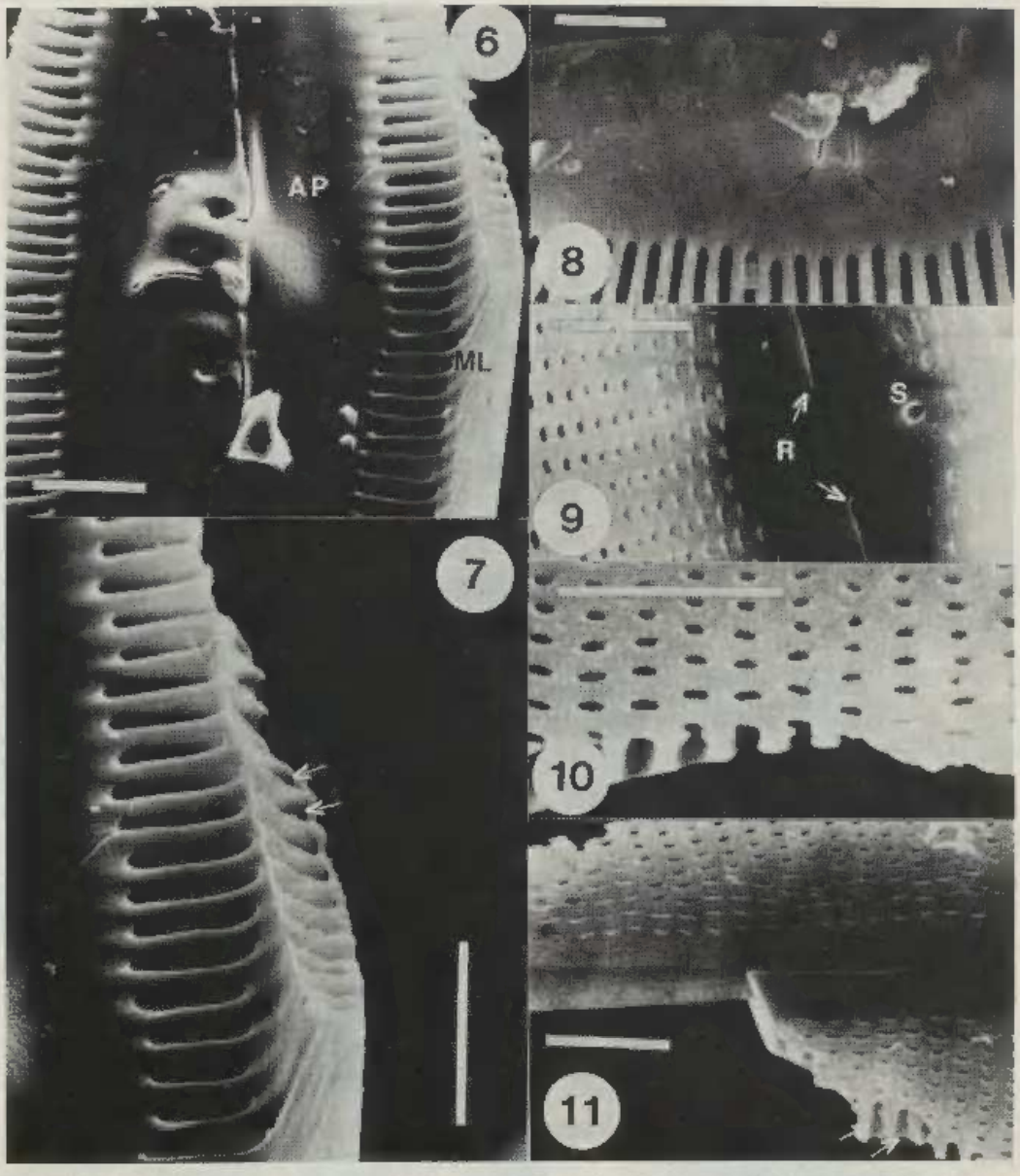

Plate 2 : *Gomphoneis cantalica*. — All figures SEM. Fig. 6-8, Internal views, fig. 9-11, External views. Fig. 6. View of valve fragment, showing expanded axial plate (AP), interstriae, marginal lamina (ML) and central nodule with stigma opening and recurved proximal raphe ends. Scale bar : 5 µm. Fig. 7. View of valve margin, showing chambers (arrows) formed between outer wall and internal marginal lamina. Scale bar : 5 µm. Fig. 8. Central nodule with recurved raphe ends and two slit-like stigmata openings (arrows). Scale bar : 5 µm. Fig. 9. Central area showing slightly enlarged raphe ends (R) and rounded stigma opening (S). Also visible are the ellipsoidal puncta. Scale bar : 5 µm. Fig. 10. Striae formed of ellipsoidal puncta. The puncta, visible externally and in cross section appear without occlusions. Scale bar : 5 µm. Fig. 11. Transverse section of raphe illustrating lock and key arrangement. Chambers (arrows) are formed between the outer wall and underlying axial plate. Scale bar : 5 µm.

glass coverslips. For light microscopy, coverslips were mounted in Hyrax and viewed with a Leitz Ortholux light microscope outfitted with brightfield optics. For scanning electron microscopy, coverslips were mounted onto aluminium stubs and sputter-coated with approximately 20 nm of gold or gold-palladium. Gold coated material was viewed on a ISI Mini-SEM, while gold-palladium coated material was viewed on a ISI DS-130. Operating voltages used were 10-15 kV.

RESULTS

Although specimens of *G. cantalica* of the material investigated were fragmented, valves appeared lanceolate-clavate in shape, tapering slightly from mid-valve to rounded poles (Fig. 1). Valve dimensions were estimated to range from 140 to 190 μm in length, and from 20 to 28 μm in breadth. Striae number 9 to 10 in 10 μm throughout the length of the valve, and are parallel in the middle portion of the valve, but become radiate at the ends. Puncta number 14 to 15 in 10 μm in each stria. Light microscopic observations indicate a highly thickened valve margin (Fig. 1). The raphe is filamentous and laterally expanded, with distal raphe ends curving opposite the side of the valve containing the stigma (Fig. 1). The apical pore field (APF) is bilobed, with the distal raphe end curving between the lobes (Fig. 2). Longitudinal lines are evident at the central part of the valve (Fig. 1).

A wide axial plate (Fig. 3) is the most striking internal valve feature shown with SEM. The axial plate appears widest at the middle portion of the valve and tapers towards the poles. Visible also is the central nodule and numerous interstriae (*sensu* ROSS et al., 1979) which are oriented perpendicular to the axial plate (Figs. 3, 6). Labiate-like helictoglossae are located at both the headpole and footpole (Figs. 3, 4; 5, respectively). Also noted at the headpole is a short pseudo-septum (Fig. 4). At the footpole the axial area becomes cruciate, forming a divided APF (Fig. 5). From the axial area the axial plate expands towards the valve margin, terminating at a distance just greater than half way to the margin (Fig. 3, 6). Chambers are formed between the axial plate and overlying outer portion of the wall. Beyond the axial plate laterally, narrow interstriae are evident and directed toward the margin (Figs. 6-8). Just prior the margin, the interstriae coalesce to form a thickened marginal lamina (Figs. 6, 7). As with the axial plate, chambers are formed between the outer wall and the lamina (Figs. 4, 6, 7). At the central nodule the raised, slit-like opening of the stigma, and recurved proximal raphe ends are present (Fig. 6, 8). One (Fig. 6) or two (Fig. 8) stigmata openings may be present.

Externally, puncta appear as elongate holes, without any apparent external flaps (*sensu* MANN, 1981) or occlusions (Figs. 9-11). Proximal raphe ends that appear slightly widened, and a rounded stigma are located in the central area (Fig. 9). Transapical views of the puncta near the axial area show chambers formed between the valve face, interstriae and axial plate (Figs. 10, 11). A trans-

apical view of the raphe indicates it is of the key and slot type (*sensu* KRAMMER, 1982a) (Fig. 11).

Girdle bands of any kind, either attached to or detached from valves or valve fragments could not be identified.

DISCUSSION

LM and SEM observations presented here are in close agreement with the dimensions and general valve shape described by Brun and Héribaud (*in* HÉRIBAUD, 1893), CLEVE (1894) and SCHMIDT (1899) for *G. cantalica*. These observations also suggest a close relationship between *G. cantalica* and classical *Gomphoneis* species. Shared features include a prominent central nodule, one or more stigmata, recurved proximal raphe ends, presence of a pseudoseptum at the headpole lip-like helictoglossae at both poles and longitudinal lines formed by an axial plate. All of these features have been previously demonstrated for *G. mammilla* (Ehrenb.) Cleve (1894) (KOCIOLEK and ROSEN, 1984). The feature of a marginal lamina, present in *G. cantalica*, was not discussed or shown for *G. mammilla* (KOCIOLEK and ROSEN, 1984), however recent reinspection of *G. mammilla* indicates a marginal lamina is present (pers. obs.). The apparent unoccluded nature of the puncta, being without external or internal flaps is shared by *G. mammilla* (KOCIOLEK and ROSEN, 1984), as well as *Gomphonema olivaceum* (Lyngb.) Kütz. (HELMCKE and KRIEGER, 1953; DRUM, 1969; DAWSON, 1974; GERMAIN, 1981), *G. quadripunctatum* (Østr.) Wisl. (DAWSON, 1974), *G. tetrastigmatum* Horikawa and Okuno (OKUNO, 1974) and *G. olivaceoides* Hust. (GERLOFF and HELMCKE, 1977; CARTER and BAILEY-WATTS, 1981), and is unlike that found in *G. parvulum* (Kütz.) Kütz (1849) (DAWSON, 1972), *G. gracile* Ehrenb. (1838) (SCHOEMAN et al., 1984), and similar *Gomphonema* species. Absence of identifiable girdle bands negates comparison with SCHMIDT's (1899, Fig. 2) observation of an unornamented girdle region in *G. cantalica*. Almost all gomphonematoidean (*Didymosphenia* M. Schm. (1899), *Gomphonema, Gomphoneis, Rhoicosphenia* Grunow) species have been shown to possess punctate girdle bands. Based on the ultrastructural features discussed here, *G. cantalica* would appear best placed in the genus *Gomphoneis*.

As indicated by both HUSTEDT (1935) and SCHMIDT (1899), the nature of the chambered areas suggests a relationship with members of the genus *Pinnularia*. In many *Pinnularia* species, the axial plate is expanded from the axial area, then terminates to expose interstriae internally. At a distance from the margin on the valve, another subtending lamina forms and extends from the valve face over the mantle (JACKSON, 1980; COX and ROSS, 1981; KRAMMER, 1982b). This results in chambers being formed between the valve surface and underlying laminae both from the axial area to the interstriae, and from the interstriae over the mantle. The area not underlain by the axial plate is delineated by two longitudinal lines on either side of the axial area formed by the edges of the

laminae. In *G. cantalica* the axial plate is well-developed, but the marginal lamina does not appear until almost the valve margin. This condition in *G. cantalica* produces the image of longitudinal lines on either side of the axial area positioned near midvalve. and a much-thickened valve margin,as depicted by SCHMIDT (1899). These observations do not correspond to HUSTEDT's (1935) illustration and description of two closely placed longitudinal lines positioned midway between the axial area and margin. The condition in *G. cantalica* differs from that described for *Gomphonema transylvanicum* Pant. which appears to possess longitudinal lines produced from underlying silica at the margin only (KRAMMER, 1982b).

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